The family Tillyardembiidae Zalessky, 1938 and the system of the plecopteroid insects

Семейство Tillyardembiidae Zalessky, 1938 и система надотряда Plecopteroidea

Danil S. Aristov¹ & Alexandr P. Rasnitsyn^{1, 2} Д.С. Аристов, А.П. Расницын

- ¹ Paleontological Institute, Russian Academy of Sciens, Profsoyuznaya, 123, 117997 Moscow, Russia. E-mail: danil_aristov@mail.ru; rasna36@yahoo.com.
- Палеонтологический институт РАН, Профсоюзная ул. 123, 117997 Москва, Россия.
- ² Natural History Museum, London, SW7 5BD, England.

KEY WORDS: fossil insects, phylogeny, taxonomy, Grylloblattida, Eoblattida, Tillyardembiidae, Perlida, Plecoptera, Permian, Carboniferous.

КЛЮЧЕВЫЕ СЛОВА: ископаемые насекомые, филогения, систематика, Grylloblattida, Eoblattida, Tillyardembiidae, Perlida, Plecoptera, Пермь, Карбон.

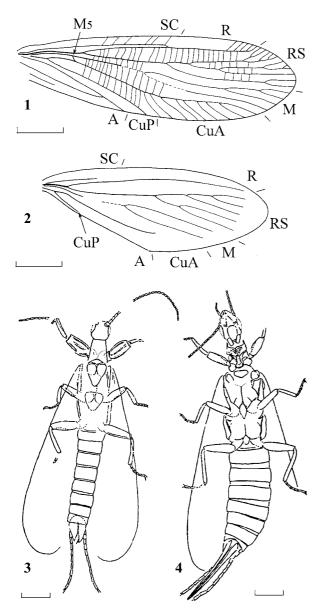
ABSTRACT. The family Tillyardembiidae is limited to two genera (Tillyardembia G.Zalessky, 1937 and Kungurembia Aristov, 2004) and four species (T. antenaeplana G.Zalessky, 1937, T. ravisedorum Vilesov et Novokshonov, 1993, K. brevicervix Aristov, 2004, and K. pallida Aristov, 2004), all from the Early Permian of Urals, Russia, and transferred from the order Grylloblattida to the previously strictly Carboniferous order Eoblattida close to the family Spanioderidae. Sister group relationship is inferred for Tillyardembiidae and stoneflies (order Perlida). Tshekardembia Novokshonov, 1995 with the only species T. sharovi Novokshonov, 1995 is transferred from Tillyardembiidae to Ivapteridae, and Permedax Aristov, 2004 with the sole species P. effertus Aristov, 2004 based on a fossil nymph is returned from Tillyardembiidae back to Grylloblattida incertae sedis.

РЕЗЮМЕ. Семейство Tillyardembiidae ограничено в составе двумя родами (Tillyardembia G.Zalessky, 1937 и Kungurembia Aristov, 2004) и четырьмя видами (T. antenaeplana G.Zalessky, 1937, T. ravisedorum Vilesov et Novokshonov, 1993, K. brevicervix Aristov, 2004 и К. pallida Aristov, 2004) из ранней перми Урала и перенесено из отряда Grylloblattida в ранее целиком карбоновый отряд Eoblattida, где сближено с семейством Spanioderidae. Сестринской группой тильярдембий, вероятно, являются веснянки (отряд Perlida). Tshekardembia Novokshonov, 1995 с единственным видом Т. sharovi Novokshonov, 1995 перенесена из Tillyardembiidae в Ivapteridae, а Permedax Aristov, 2004, также с единственным видом P. effertus Aristov, 2004, описанным по нимфе, возвращён из Tillyardembiidae в Grylloblattida incertae sedis.

Introduction

The genus Tillyardembia G.Zalessky, 1937 with two species T. antenaeplana G.Zalessky, 1937 and T. biarmica G.Zalessky, 1937 have been described from the upper Lower Permian (Kungurian) deposits of Tshekarda locality in the Middle Urals [Zalessky, 1937]. Next year the same author has proposed the new family Tillyardembiidae and has not specified its ordinal position [Zalessky, 1938]. Two years later Martynov has described the new family Permocapniidae with the genus and species Permocapnia brevipes Martynov, 1940 from the same locality and has attributed it to the order Paraplecoptera [Martynov, 1940]. Zalessky [1950] has synonymized Permocapniidae under Tillyardembiidae and Permocapnia under Tillyardembia and has described the additional species T. minuta G.Zalessky, 1950. A new order Epiembioidea has been created there to house Tillyardembiidae as well [Zalessky, 1950]. Later on all the species within *Tillyardembia* have been synonymized under antennaeplana G.Zalessky, 1938 (Figs 1–4), the new species T. ravisedorum Vilesov et Novokshonov, 1993 has been described (Fig. 5), and morphology of the genus have been studied in details by Vilesov and Novokshonov [1993]. The new genus Kungurembia Aristov, 2004 with two species K. brevicervix Aristov, 2004 (Figs 6-7) and K. pallida Aristov, 2004 (Figs 8-9) from Tshekarda have been added to the family by Aristov [2004]. Hence the family embrace currently two genera with four species from one and the same locality of the latest Early Permian age.

One more genus from Tshekarda, *Sylvardembia* Novokshonov, 1997, and the genus *Barmaleus* Novokshonov, 1997 from same locality and the Middle Permian Soyana locality, north in the European Russia, have



Figs 1–4. *Tillyardembia antennaeplana*: 1 — forewing; 2 — hindwing (original restoration based on specimens PIN 1700/794, 1451, 1482, 1822, 4285; 4987/664, 668, 686, 688, 710); 3 — male body from above; 4 — female body from below (restored by Vilesov et Novokshonov, 1993); Tshekarda, Russia, Lower Permian. Scale bar in figures 1–6, 9 is 2 mm. Venational symbols are customary.

Рис. 1—4. *Tillyardembia antennaeplana*: 1 — переднее крыло; 2 — заднее крыло (оригинальная реконструкция по экз. ПИН, №№ 1700/794, 1451, 1482, 1822, 4285; 4987/664, 668, 686, 688, 710); 3 — тело самца сверху; 4 — тело самки снизу, реконструкция [из Vilesov et Novokshonov, 1993]; Чекарда, нижняя пермь России. Длина масштабной линейки на рис. 1—6, 9 соответствует 2мм. Обозначения жилок стандартные.

been described as members of Tillyardembiidae as well [Novokshonov, 1997a, b]. However, later they were transferred to the family Sylvardembiidae [Novokshonov, 2000]. *Tshekardembia* Novokshonov, 1995 with the only species *T. sharovi* Novokshonov, 1995 (Figs 10–11) has been ascribed to Tillyardembiidae as well

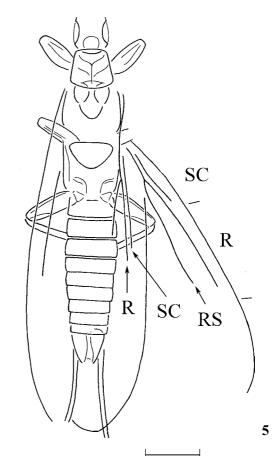
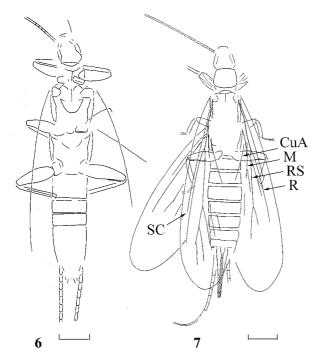


Fig. 5. *Tillyardembia ravisedorum*, holotype PIN, 2/183, general appearance of male; Tshekarda, Russia, Lower Permian (orig.). Рис. 5. *Tillyardembia ravisedorum*, голотип ПИН, № 2/183, общий вид самца; Чекарда, нижняя пермь России (ориг.).

[Novokshonov, 1995]. However, its re-study has demonstrated M forking as early as in the basal wing third, and CuA splitting into CuA₁ and CuA₂ in its basal quarter, the features not at all characteristic of Tillyardembiidae which has M forking at the wing midlength, and CuA lacking individualized CuA₁ and CuA₂ (Fig. 1). The combination of the above characters with the pronotum lacking paranota is known otherwise only in the family Ivapteridae [Aristov, 2009]. That is why *Tshekardembia* is transferred herein to the Ivapteridae.

One more genus formerly included into Tillyardembiidae is the monotypical *Permedax* Aristov, 2004 (Fig. 12), a nymph first described as Grylloblattida incertae sedis [Aristov, 2004] and later transferred to Tillyardembiidae based on its similarity with *Tshekardembia* [Aristov et al., 2006]. Additional study of the type and only species *P. effertus* Aristov, 2004 has reveal long hind legs with the short tarsus hardly expectable of Tillyardembiidae whose adults have their legs short with proportional and not shortened tarsus. Under these observations, *Permedax* is moved herein back to Grylloblattida incertae sedis.

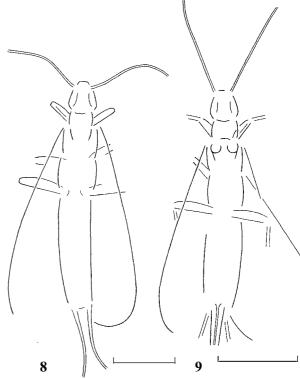


Figs 6–7. *Kungurembia brevicervix*: 6 — paratype PIN 4987/16, general appearance of male (from Aristov, 2004); 7 — female (orig., body restored based on holotype PIN 1700/796 and paratype PIN 1700/952). Tshekarda, Russia, Lower Permian.

Рис. 6–7. *Kungurembia brevicervix*: 6 — паратип ПИН, № 4987/16, общий вид самца (из Aristov, 2004); 7 — самка (реконструкция тела на основе голотипа ПИН, № 1700/796, и паратипа ПИН, № 1700/952; Чекарда, нижняя пермь России (ориг.).

Tillyardembiid abundance in the Tshekarda (some 5% of all insect fossils collected there) and structure of their wings with weak veins and convex fore margin jointly attest them as weak fliers frequented near coastline or maybe swarming above the water but otherwise hardly tightly connected to a water body. At any case, absence of the nymph fossils indicates terrestrial and not aquatic development of Tillyardembiidae. In respect to the feeding habits, tillyardembiids were probably saprophagous with the facultative pollinivory [Afonin, 2000].

Abundance of the tillyardembiid fossils made them one of the best studied insects of Tshekarda. At least the body structure of males and females of Tillyardembia antennaeplana is restored in some details [Vilesov & Novokshonov, 1993]. Nevertheless the taxonomic position of the family has never been unquestionable. It was included into orders Paraplecoptera (= Grylloblattida) [Martynov, 1940; Sharov, 1962], Epiembioidea (Zalessky, 1950), Protorthoptera (= Paoliida + Eoblattidae + Grylloblattida + Hypoperlida + Blattinopseida) [Carpenter, 1992], Grylloblattida [Rasnitsyn, 1980; Vilesov & Novokshonov, 1993; Storozhenko, 1997a, b, d, 1998, 2002; Aristov, 2004], that is, in our current terms, it looks like an ordinary grylloblattidan family. However, both Sharov [1962] and Carpenter [1992] placed it close to the carboniferous Geraridae whose separate



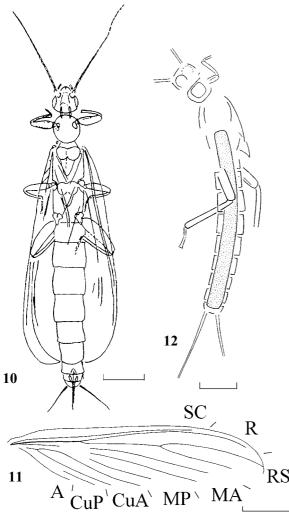
Figs 8–9. *Kungurembia pallida*: 8 — holotype PIN N 4987/19, general appearance of male; 9 — paratype PIN N 4987/21, general appearance of female. Tshekarda, Russia, Lower Permian (from Aristov, 2004).

Рис. 8–9. *Kungurembia pallida*: 8 — голотип ПИН, № 4987/19, общий вид самца; 9 — паратип ПИН, № 4987/21, общий вид самки; Чекарда, нижняя пермь России (из Aristov, 2004).

position in respect to the ordinary grylloblattideans already raise little doubts [cf. Rohdendorf & Rasnitsyn, 1980; Kukalová-Peck & Brauckmann, 1992; Rasnitsyn & Quicke, 2002; Gorochov, 2001, 2004; Grimaldi & Engel, 2005]. Particularly, Sharov [1961, 1962, 1968] and Gorochov [2001, 2004] present serious evidence that Geraridae (= Sthenaropodidae) represent a basal taxon of the orthopteroid insects. More close analysis of Tillyardembiidae suggests revision of its ordinal position as well.

Characteristic of Tillyardembiidae are absence of the pronotal paranota, SC ending to R, and M splitting at near wing midlength distal of the RS base (Figs 1–4). Judging from wings of the most archaic winged insects, the order Paoliida, these characters are possibly ground plan for the Pterygota. Unlike Tillyardembiidae, Grylloblattida has SC ending into C, and their M forks as basal as basal third of wing. Re-study of *T. antennae-plana* shows the forewing anal area modified into a distinct even though rather narrow clavus as well as the convex hindwing CuA (grylloblattid insects have anal area not differentiated clavus-like, and hindwing CuA concave). This makes problematic accommodation of the family within the order Grylloblattida.

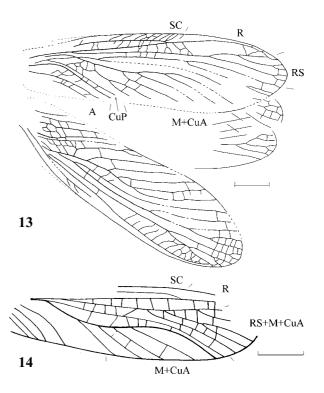
The above set of characters (excluding the convex hindwing CuA) parallels only to the Carboniferous orders Paoliida and particularly Eoblattida. Paoliida



Figs 10–12. *Tshekardembia sharovi*, holotype, PGU, N 1/246: 10 — general appearance of female (from Novokshonov, 1995); 11 — forewing restored (orig.); Tshekarda, Russia, Lower Permian; 12 — *Permedax effert*us, nymph restored based on holotype, PIN, N 1700/1988, and paratype PIN, N 1700/1987; Tshekarda, Russia, Lower Permian (orig.).

Рис. 10—12. *Tshekardembia sharovi*, голотип ПГУ, № 1/246: 10 — общий вид самки (из Novokshonov, 1995); 11 — реконструкция переднего крыла; Чекарда, нижняя пермь России (ориг.); 12 — *Permedax effert*us, реконструкция нимфы на основе голотипа ПИН, № 1700/1988 и паратипа ПИН, № 1700/1987; Чекарда, нижняя пермь России (ориг.)

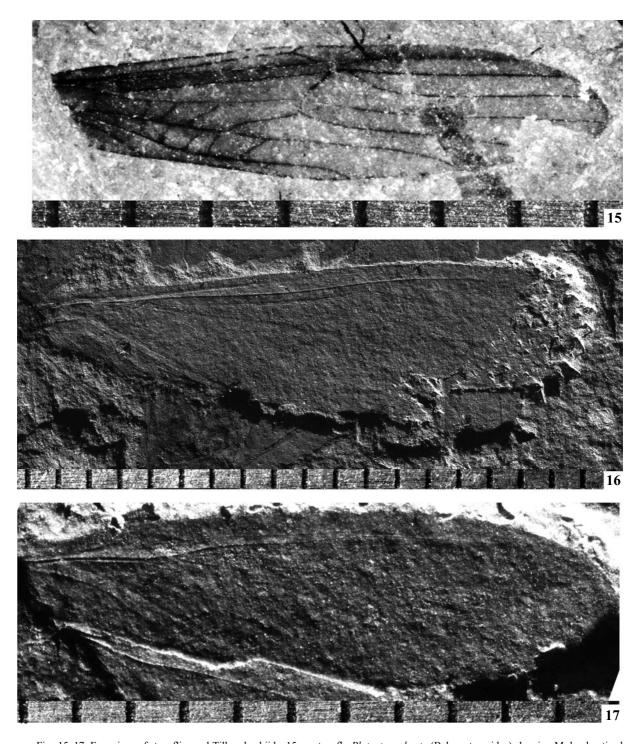
differs from Tillyardembiidae in many respects [archaic rich and rather irregular venation, absolutely different general habits with very long legs and antennae; cf. Rasnitsyn, 2002] but most deeply in having no hind wing anal lobe which would tuck down under the remigium. This absence is probably primary, that is, the plesiomorphic absence rather than a secondary reduction [Rasnitsyn, 2002]. That is why close relatedness of Paoliidae and Tillyardembiidae looks less likely. Eoblattidans [as interpreted by Rasnitsyn, 2002] and particularly the family Spanioderidae (Figs 13–14) are much more similar. The latter family differs from the rest eoblattidans in a set of traits including the comparative-



Figs 13–14. Representatives of the Family Spanioderidae: 13 — *Miamia bronsoni*, neotype FMNH PE 31967, general appearance (from Bethoux, 2008); 14 — *Dieconeura arquata*, forewing restored based on the holotype USNM, N 38146 (modified after Burnham, 1986); Mazon Creek, Illinois, USA, Middle Carboniferous. Scale line 5 mm.

Рис. 13—14. Представители семейства Spanioderidae: 13 — *Miamia bronsoni*, неотип FMNH PE 31967, общий вид (из Bethoux, 2008); 14 — *Dieconeura arquata*, переднее крыло, реконструкция на основе голотипа USNM, № 38146 (из Вигл-ham, 1986 с изменениями); Мэзон Крик, средний карбон США. Длина масштабной линейки соответствует 5 мм.

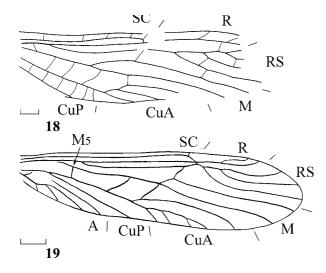
ly narrow costal space, proximal position of RS which runs only moderately close to R (not as tight and for as long distance as in *Eoblatta* Handlirsch, 1906, *Ctenop*tilus Lameer, 1917, and their relatives), and M fused with CuA for a distance in a place of the former M₅ [Burnham, 1986; Bethoux, 2008]. Most of the above characters are shared with Tillyardembiidae, except that the latter has M and CuA connected with M, and not fused for a distance subbasally. Additionally, Tillyardembiidae are similar to Spanioderidae in having large head with big eyes, early origin of RS, late forking of M, CuA with the backward comb and without basal blind branchlets, and simple CuP. Tillyardembiidae differs from Spanioderidae in having RS well distant from R, M neither convex nor concave and with the stalk desclerotized distally and MP stalk de-sclerotized basally, M₅ present, and CuA branching only its distal quarter. Tillyardembiidae differs from all Eoblattida also in the small body size (measurable in millimeters rather than in centimeters which is the case of Eoblattida) and in having long and strong ovipositor. However, long ovipositor is the rare occasion in the Carboniferous insects



Figs 15–17. Forewings of stoneflies and Tillyardembiids: 15 — stonefly *Plutopteryx beata* (Baleyopterygidae) showing M desclerotized before and after forking into MA and MP (spec. PIN, N 4023/77, Middle Permian of Bayan Teeg in Mongolia); 16 — stonefly *Perlopsis filicornis* (Perlopseidae), showing developed clavus (spec. PIN, N 1700/1221, Tshekarda, Russia, Lower Permian); 17 — the same for *Tillyardembia antennaeplana* (spec. PIN, N 4987/668, Tshekarda, Russia, Lower Permian). Scale unit 1 mm.

Рис. 15—17. Передние крылья веснянок и тильярдембий: 15 — веснянки *Plutopteryx beata* (Baleyopterygidae), демонстрирующее десклеротизацию М в области развилка (экз. ПИН, №4023/77, средняя юра, карьер Баян-Тег, Монголия); 16 — веснянки *Perlopsis filicornis* (Perlopseidae; экз. ПИН, №1700/1221; Чекарда, Россия, нижняя пермь) с выраженным клавусом; 17 — то же у *Tillyardembia antennaeplana* (экз. ПИН, №4987/668; Чекарда, Россия, нижняя пермь). Цена деления линейки 1 мм.

(except possibly the true cockroaches) registered with any certainty in no Paoliida and Eoblatttida. Small body size and long ovipositor of Tillyardembiidae could be easier interpreted as autapomorphies of the family which do not prevent its transfer to the order Eoblattidae as the general balance of characters suggests. It should be



Figs 18–19. Forewings of fossil stoneflies: 18 — *Stenoperlidium permianum* (Eustheniidae) (orig., based on holotype; Belmont, Australia, Upper Permian); 19 — *Cristonemura porrecta* (Perlariopseidae), (orig., based on holotype PIN, N 2244/2209; Madygen, Kyrgyzstan, Middle or Upper Triassic).

Рис. 18—19. Передние крылья ископаемых веснянок: 18 — *Stenoperlidium permianum* (семейство Eustheniidae), голотип; Бельмонт, верхняя пермь Австралии (ориг.); 19 — *Cristonemura porrecta* (семейство Perlariopseidae), голотип ПИН, № 2244/2209, реконструкция переднего крыла; Мадыген, средний или верхний триас Киргизии (ориг.).

noted however that the limits and system of Eoblattida are insufficiently explored and need much work to be invested to.

Worth considering is also the similarity between Tillyardembiidae and the stoneflies (Order Perlida), particularly in respect to their forewing venation. They share SC ending on R, the early origin and pectinate branching of RS, distal position of the basal M fork, preserved M_s (called arculus in stoneflies), and distal branching of CuA which is archetypically with the backward comb. Stoneflies are generally considered originated from the order Grylloblattida [Rasnitsyn, 1980; Hennig 1981; Rasnitsyn 2002; Storozhenko 2002; Grimaldi & Engel, 2005: fig. 6.7] Some other authors descend them from Eoblattida [Gorochov, 2004], or else conclude that "Palaeozoic stoneflies are so distinct from other contemporaneous or older polyneopterous taxa that, based on our fossil record, no other taxon can reliably be pointed out as potential sister-group" [Béthoux, 2005: 23]. Tillyardembiidae along with several other grylloblattidean families have already been indicated as possibly related to the stoneflies [Rasnitsyn, 1980: 149]. In addition to the similarities listed earlier in this paragraph, M and MP de-sclerotized in vicinity of the fork is known for the Paleozoic stoneflies (Fig. 15) and the anal area transformed into the clavus, that is, with A, high convex above the deeply concave CuP (Figs 16–17) and so more free movable in respect to the rest wing blade [cf. Gorochov, 2004]. Among the fossil stoneflies, more similar to Tillyardembiidae are the Permian Eustheniidae (Fig. 18) and Mesozoic Perlariopseidae (Fig. 19) which differ in having the pre-radial space narrower at the level of SC apex, RS angled and approaching R at r-rs crossvein (particularly so in Perlariopseidae), MA and MP simple, the CuA comb shorter (more or less disorganized or directed forward in Perlariopseidae), and the crossvein system much differentiated [cf. Sinitshenkova, 1987].

Based on the forewing only, it is not always easy to discriminate tilyardembiids and stoneflies. The formers have the wing fore margin convex unlike all stoneflies but the Permian *Properla* Sharov, 1961 (Palaeoperlidae). RS is smooth in Tillyardembiidae in contrast to the vast majority of stoneflies which have it angled at rrs crossvein. RS and M are more richly branched in Tillyardembiidae than in all or almost all stoneflies. The hind wing and body structures yields more reliable diagnostic features which are unfortunately not so commonly available for the fossils. Tillyardembiids differ strikingly from stoneflies in having hindwing M free of CuA subbasally, ocelli lost, tarsi 5-segmented, and females bearing long and rather thick ovipositor. Tillyardembiid nymphs are unfortunately unknown; yet it is possible hypothesize their terrestrial habits and 5-segmented tarsi unlike the aquatic development (with few apomorphic exceptions) and 3-segmented tarsi of the stonefly nymphs.

The known Tillyardembiidae (genera *Tillyardembia* and *Kungurembia*) are too much specialized to hypothesize them ancestral in respect to the stoneflies. Rather, the latter are monophyletic with Tillyardembiidae and form its sister group. Origin of stoneflies was probably a result of adaptation to aquatic development which influenced somehow oligomerization of the tarsal segments and reduction of the ovipositor. The evident improvement of the flight quality of the stonefly wings might also depend on the aquatic development which needs reaching more remote and specific habitats.

Hence, Tillyardembiidae and stoneflies are here hypothesized originating jointly from an eoblattid ancestor supposedly related to Spanioderidae and independently of the line leading to the order Grylloblattida. This hypothesis, first erected by Gorochov [2004], implies Eoblattida to be included to the superorder Perlidea (= Plecopteroidea; Rasnitsyn & Quicke [2002], treated eoblattideans as Gryllones incertae superordinis). This nomenclatury act affects the taxonomic position of some other orders and superorders of the gryllonean (polyneopteran) insects, because Eoblattida has been hypothesized by Rasnitsyn & Quicke [2002] to be the stem group of the Infraclass Gryllones.

The orthopteroid insects (Superorder Gryllidea) are less affected if to follow Gorochov [2004] in that the stem orthopteroids was a group closely related to the family Geraridae which forms the suborder Gerarina within the order Mesotitanida (= Titanoptera). Besides the Paleozoic gerarids and the traditional, mainly triassic titanopterans, the order additionally embraces the enigmatic contemporary Mantophasmatidae: Gorochov treats them as a distinct superfamily within the suborder Mesotitanina. As a result, the orthopteroid insects appear taxonomically and, by inference, phylogenetically independent of

the plecopteroid insects including Eoblattida.

The case of the blattoid insects (Superorder Blattidea) is more complicated. These are hypothesized originated from Eoblattida based on presence of the wide paranota and well delimited wide clavus in the fore wings of some eoblattidans (best developed in Eoblatta). Previously, the wide pronotal paranota are considered to be a pterygote ground plan character. However, the most old and primitive insects, the Paoliidae are found lacking them (contrary evidence presented by Ilger & Brauckmann, 2008 seems inconclusive), as well as many other higher taxa of the Carboniferous insects including the majority of Eoblattida [cf. Rasnitsyn & Quicke, 2002: figs. 353–363]. This means that the wide paranotal ring well might be aquired apomorphically by cockroaches, grylloblattidans, few eoblattidans, and palaeodictyopteroids. The last case could be only independent (homoplastic), but the nature of similarity between the former three groups is obscure in terms of synapomorphy vs. homoplasy. The problem is that few eoblattidans have both cockroach characters mentioned (paranotal ring and clavus) present at once (e.g., *Eoblat*ta, Polyernus Scudder 1885). Many others have only clavus but not paranotal rings (e.g., Stenoneuridae, Cnemidolestideae, etc.). These additionally show R and RS closely approximated, the character shared with Eoblatta. Other characters are involved into the puzzle as well, so as the latter needs much more efforts to be resolved. Until relationships between the members of the confusing assemblage called Eoblattida are reasonably clarified, we tentatively keep this group as an order within the Superorder Perlidea and separate of Blattidea, waiting for clarification of the roots of the latter, either within Eoblattida or not. It looks likely that this clarification will result in further splitting of the eoblattidans.

Taxonomy

Order Eoblattida Handlirsch, 1906

Family Tillyardembiidae G.Zalessky, 1938

- Tillyardembiidae: G.Zalessky, 1938: 64; Sharov, 1962: 124; Rasnitsyn, 1980: 152; Carpenter, 1992: 123; Vilesov, Novokshonov, 1993: 65; Storozhenko, 1997a: 63; 1997b: 8; 1997d: 24; 1998: 91; 2002: 279; Aristov, 2004: 115.
- = Permocapniidae: Martynov, 1940: 20 (synonimized by G.Zalessky, 1950: 41–60).

TYPE GENUS. Tillyardembia G.Zalessky, 1937.

DIAGNOSIS (Figs 1–9, 17). Head with big eyes and thick, long antennae and with no ocelli. Legs not long, fore and mid pairs of equal length or mid the shortest, hind legs longer, male fore femora can be incrassate, tarsus 5–segmented. SC meeting R. R and RS running at distance, RS starting at wing basal quarter, branching since wing midlength. M not fused with CuA subbasally, M₅ present, M forking at wing midlength distad of RS base, M stalk distally and MP basally desclerotized but not much impressed. CuA lacking splitting into individualized CuA₁ and CuA₂, comb-like branching since wing midlength. CuP simple. Anal area forming distinct but rather narrow clavus (CuP well concave, and A₁

distinctly elevated above it). Hind wing with RS, M, and CuA free basally. Ovipositor long, strong, cerci long, multisegmented. Male gonocoxae symmetrical.

COMPOSITION. Two genera from the Lower Permian of Russia.

COMPARISON. Most similar to Spanioderidae but differs in having R and RS running well distant of each other, M and CuA both branching more distally, and M₅ present (M and CuA not fused subbasally).

Identification key to family Tillyardembiidae G.Zalessky, 1938

- 1 (4) Pronotum elongate, costal and subcostal space of subequal width at wing midlength
- 2 (3) Male fore femur 1,9–2,1 times as long as wide, body length 11,5–15 mm in male, 11,5–18 in female

- ... *T. ravisedorum* Vilesov et Novokshonov, 1993 (Fig. 5) 4 (1) Pronotum as long as wide, costal space wider that

ACKNOWLEDGEMENTS. The present study is supported in part by the Presidium RAS Program "Origin and evolution of Biosphere" and the Russian Foundation for Basic Research Grant # 09-04-01241

References

- Afonin S.A. 2000. Pollen grains of the genus *Cladaitina* extracted from the gut of the Early Permian insect *Tillyardembia* (Grylloblattida) // Paleontological Journal. Vol.34. No.5. P.575–579.
- Aristov D.S. 2004. The Fauna of Grylloblattid Insects (Grylloblattida) of the Lower Permian Locality of Tshekarda // Paleontological Journal. Vol.38. Suppl.2. P.80–145.
- Aristov D.S. 2009. [A new family of order Grylloblattida (Insecta) from the Middle Permian of Russia] // Paleontologicheskij Zhurnal. No.2. P.59–63 [in Russian, English translation Paleontological Journal.Vol.43. P.178–182].
- Aristov D.S., Novokshonov V.G., Pan'kov N.N. 2006. [Taxonomy of the fossil grylloblattid nymphs (Insecta: Grylloblattida)] // Paleontologicheskij Zhurnal . No.1. P.75–85 [in Russian, English translation Paleontological Journal. Vol.40 P.79–89].
- Béthoux O. 2005. Wing venation pattern of Plecoptera (Insecta: Neoptera) // Illiesia. Vol.1. No.9. P.52–81.
- Béthoux O. 2008. Revision and Philogenetic Affinities of the Lobeattid Species *bronsoni* Dana, 1864 and *sylvatica* Laurentiaux et Laurentiaux-Vieira, 1980 (Pensilvanian; Archeorthoptera) // Artropod Systematics & Phylogeny. Vol.66. No.2. P.145–163.
- Burnham L. 1986. Revisionary studies on Upper Carboniferous insects in the order Protorthoptera. PhD thesis, Cornell University. 178 p.
- Carpenter F.M. 1992. Treatise on Invertebrate Paleontology. Pt. R. Arthropoda 4. Vol. 3: Superclass Hexapoda. Boulder and Lawrence. 655 pp.
- Gorochov A.V. 2001. On the higher classification of the Polyneoptera (short course) // Acta geol. leopold. Vol.24. Nos.52/53. P.11–56.

- Gorochov A.V. 2004. [Primitive Titanoptera and the Early Evolution of the Polyneoptera] // Chteniya pamyati N.A. Kholodkovskogo, Iss. 57, No. 1, P.1-54 [in Russian].
- Grimaldi D. & Engel M.S. 2005. Evolution of the insects. Cambridge University Press. xv + 755 pp.
- Hennig W. 1981 Insect Phylogeny. New York, USA: Wiley &
- Sons. xxii + 514 pp.
 Ilger J.M., Brauckmann C. 2008. Evidence for prothoracic winglets in Kochopteron hoffmannorum from Hagen-Vorhalle ("basal Neoptera", early Carboniferous; Germany // Entomologia generalis. Vol.31. P.279-285.
- Kukalová-Peck J., Brauckmann C. 1992. Most Paleozoic Protorthoptera are ancestral hemipteroids: Major wing braces as clues to a new phylogeny of Neoptera (Insecta) // Canadian Journal of Zoology. Vol.70. P.2452-2473.
- Martynov A.V. 1940. [Permian fossil insects from Tschekarda] // Trudy Paleontologicheskogo Instituta AN SSSR. Vol.11. No.1. P. 5-62 [in Russian].
- Novokshonov V.G. 1995. [New fossil insects (Insecta) from the Kungurian deposits of the Middle Urals] // Paleontologicheskij Zhurnal. No.3. P.61-67 [in Russian, English translation Paleontological Journal. Vol.29. P.76-85].
- Novokshonov V.G. 1997a. [New taxa of fossil insects (Insecta) from the Lower Permian of Chekarda] // Paleontologicheskij Zhurnal. No.4. P.39-44 [in Russian, English translation Paleontological Journal. Vol. 31. P.383-388].
- Novokshonov V.G. 1997b. [New Barmaley from the Upper Permian of the Arkhangelsk Region (Insecta; Gryllobattida: Tillyardembiidae)] // Vestnik Permskogo Universiteta. Ser. Biol. No.3. P.202-205 [in Russian].
- Novokshonov V.G. 2000. [New fossil insects (Inecta: Grylloblattida, Ordinis incertis) from the Lower Permian of the Middle Urals] // Paleontologicheskij Zhurnal. No.5. P.42-47 [in Russian, English translation Paleontological Journal. Vol.34. P. 513-518].
- Rasnitsyn A.P. 1980. [Superorder Perlidea. Order Grylloblattida] // Rodendorf B.B. & Rasnitsyn A.P. (eds.). Istoricheskoye razvitie klassa nasekomykh [Historical development of the Class Insecta]. Trudy Paleontol. Inst. Akad. Nauk SSSR. Vol. 175. Moscow: Nauka. P.148-154 [in Russian].
- Rasnitsyn A.P. 2002. 2.2.2.2. Superorder Perlidea Latreille, 1802 (=Plecopteroidea Martynov, 1938) // A.P. Rasnitsyn & D.L.J. Quicke (eds.). History of Insects. Kluwer Academic Publishers, Dordrecht, The Netherlands. P.276-278.

- Sharov A. G. 1961. [Paleozoic Insects of the Kuznetsk Basin. Orders Protoblattodea and Paraplecopteral // Trudy Paleontol. Inst. Akad. Nauk SSSR. Vol. 85. Moscow: Nauka. P.157-234 [in Russian].
- Sharov A.G. 1962. [Orders Protoblattodea, Paraplecoptera] // Osnovy Paleontologii [Fundamentals of Paleontology]: Arthropoda, Tracheata, Chelicerata, Moscow: Nauka, P.116-138 [in Russian]
- Sharov A.G. 1968. [Phylogeny of the orthopteroid insects] // Trudy Paleontol. Inst. Akad. Nauk SSSR. Vol. 118. Moscow: Nauka. 218 p. [in Russian].
- Sinitshenkova N.D. 1987. [Historical development of stoneflies] // Trudy Paleontol. Inst. Akad. Nauk SSSR. Vol.221. Moscow: Nauka. 142 pp. [in Russian]
- Storozhenko S.Yu. 1997a. Fossil history and phylogeny of Orthopteroid insects // The Bionomics of Grasshoppers, Katydids, and their Kin. Oxton & New York: CAB International, P.59-82.
- Storozhenko S.Yu. 1997b. Classification of order Grylloblattida (Insecta) with description of new taxa // Far Eastern Entomologist, No.42, P.1-20,
- Storozhenko S.Yu. 1997c. [Classification and phylogeny of the order Grylloblattida] // Chteniya pam'yati Alekseya Ivanovicha Kurentsova. No.7. Vladivostok: Dal'nauka. P.21-56. [in Russian].
- Storozhenko S.Yu. 1998. [Systematics, phylogeny and evolution of the grylloblattids (Insecta: Grylloblattida)]. Vladivostok: Dal'nauka. 207 p. [in Russian].
- Storozhenko S.Yu. 2002. Order Grylloblattida Walker, 1914 // A.P. Rasnitsyn & D.L.J. Quicke (eds.). History of Insects. Dordrecht: Kluwer Acad. Publ. P.278-281.
- Vilesov A.P., Novokshonov V.G. 1993. [Permian Tillyardembiidae (Insecta, Grylloblattida)] // Paleontologicheskij Zhurnal. No.3. P.56-65 [in Russian, English translation Paleontological Journal. Vol. 27. No. 3. P.71-82].
- Zalessky G.M. 1937. Ancestor of Some Groups of the Present-day Insects // Nature. Vol.140. P.847-849.
- Zalessky G.M. 1938. Les nouveaux insects permiens de l'ordre Emboidea // Ann. Soc. Geol. Nord. Vol.63. P.62-81.
- Zalessky G.M. 1950. [Permian insects of the Sylva River basin and problems of evolution in the class Insecta. IV. New representatives of ther group Epiembioidea and the webspinner evolution] // Problemy paleontologii. Vol.1. P.41-60 [in Russian].